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MOUNTED SKELETON OF *TRICERATOPS ELATUS*

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The completion of this mount marks an important step forward in our knowledge of the Ceratopsia and especially of the genus *Triceratops*. Four outstanding points are: (1) The correct formula of the Pes in this genus; (2) The widely spread position of the fore limbs; (3) the connection of the prepubis with the posterior ribs; (4) the composition of the skeleton as a whole which, in harmony with the three-horned skull, proves that the characteristic pose is highly resistant to attack. As to point (2), while the hind limbs are vertical, as in previous mounts, the fore limbs, unlike previous mounts, stand widely apart to brace the head, with its horns and shield, against powerful attack probably from carnivorous dinosaurs of the *Tyrannosaurus* type. We shall return to the pose and work of mounting after describing the materials of which this mount is composed.

A COMPOSITE SKULL AND SKELETON

Amer. Mus. Nos. 5033, 5045, 5039, 5116 (originals); modeled parts after Amer. Mus. 970, 971 and 973.

This composition of bones belonging to four individuals and found in two states, Montana and Wyoming, renders it probable that the skull and skeleton represent more than one species, yet it appears to be correct in proportion.

ORIGINAL MATERIALS.—The basis of the mount is the skeleton Amer. Mus. 5033, found by Brown and Kaisen on the expedition of 1909, sixteen miles southeast of Lismas, Montana. This number includes two cervical, fourteen dorsal, and seven caudal vertebrae, twenty-eight ribs, a complete pelvis and sacrum, a complete right hind limb and foot, and a complete left femur.

In the same Montana locality was found Amer. Mus. 5045, a coössified series of cervical vertebrae; also from the same locality a lower jaw (Amer. Mus. 5039).

SKULL.—A beautifully preserved skull (Amer. Mus. 5116) was found by the veteran collector Charles H. Sternberg on Seven Mile Creek, Niobrara County, Wyoming, in 1909 and was presented to the American Museum by Mr. Charles Lanier.

RESTORED FORE LIMBS.—The fore limbs are restored in plaster chiefly from Amer. Mus. 970, from Hell Creek, Montana, 200 feet above Fort Pierre, and from other individuals, mostly of larger size than this skeleton, including some guidance from the National Museum mounted skeleton (Nat. Mus. 4842).

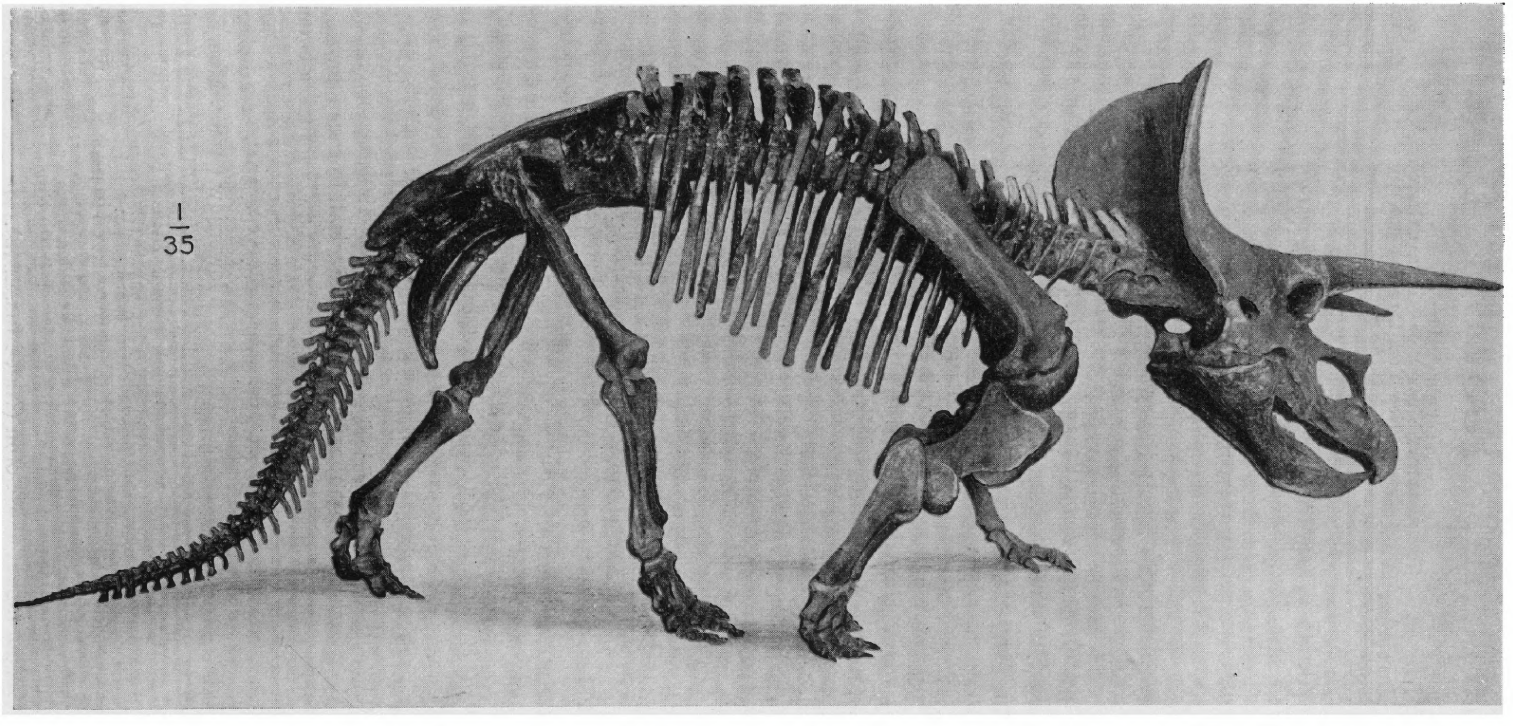

Fig. 1. *Triceratops elatus*, American Museum composite skeleton. Direct lateral view. One-thirty-fifth natural size.

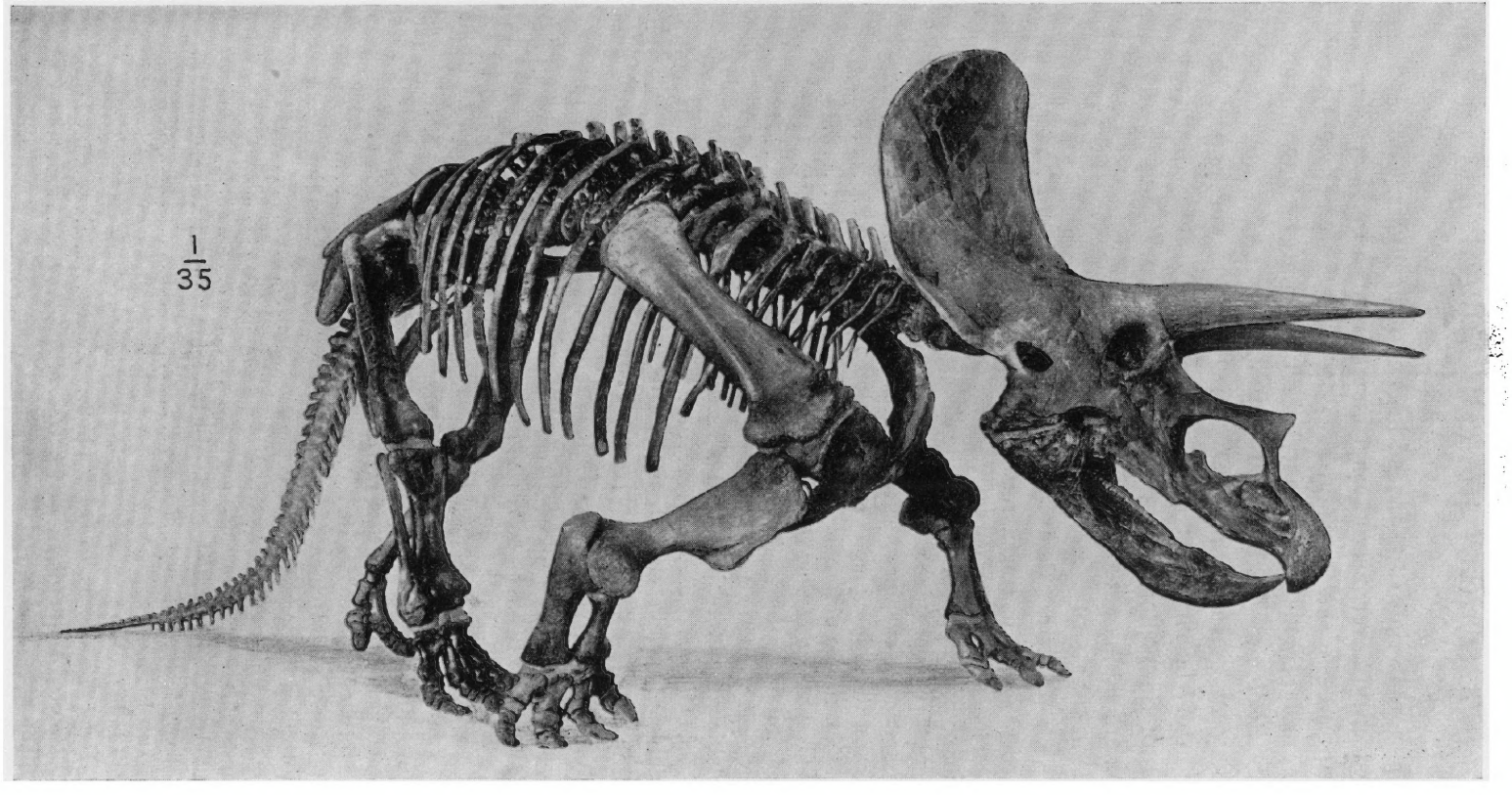

Fig. 2. *Triceratops elatus*, American Museum composite skeleton. Oblique anterior view. One-thirty-fifth natural size.

These materials were placed in the hands of Mr. Charles Lang, and the restoration, reconstruction, modeling of missing parts, and final mounting of the skeleton and skull in 1923 are chiefly his work, principally guided by his studies of living reptiles and of scores of photographs from the Zoological Park, but also by unwearying thoroughness in trying out every modification in pose, articulation of the bones, and reconstruction of the ribs that appeared possible. The discovery of the relation of the posterior thoracic rib to the prepubis by ligamentous attachment is due chiefly to him.

PRINCIPAL PROPORTIONS OF THE SKELETON IN METERS.

Vertical square of length, rostrum to tip of tail	5.80 = 19 ft. 1 in.
Total length following curves, rostrum to tip of tail	7.08
Thorax, broadest area of, opposite eleventh thoracic	1.50
Highest point of spine above coracoid	1.77
Highest point of spine at sacrum	2.165
Highest thoracic spine in vertebral column	2.305
Greatest spread of fore limb at elbows (=4-foot tread)	2.10
Greatest spread of hind limb, across pes (hind tread)	1.35
Skull, total length occipital condyles to rostrum	1.12
Vertebral column, atlas to tip of caudals	5.96
Total length of fore limb, head of humerus to distal phalanx of D.III	1.69
Total length of hind limb, head of femur to tip of ph. 4	2.23
Ratio, brachio-crural (brachio = arm, crural = leg)	76%

From the above principal measurements and with the photographs which are here reproduced to a uniform scale of one-thirty-fifth, the proportions of all parts of the skeleton may be calculated.

DETAILED MEASUREMENTS IN METERS

VERTEBRAE, TWENTY-THREE PRESACRALS, TEN SACRALS	
Total linear measurements of vertebrae, "cervicals" including total of eight centra	.83
Total linear measurements of vertebrae, "cervicals" including total of four consolidated centra	.44
Thoracics, fifteen free centra	1.74
Sacrals plus dorsosacrals, ten centra	.985
Caudals, seven original bone, thirty-eight restored, total forty-five, estimated	2.37
GIRDLES AND LIMBS	
Fore Limbs:	
Head of humerus, to D.III, ph. 3	1.69
Restored scapulo-coracoid	1.44
Humerus, head to end of condyle	.80

Radius:
Proximal to distal end..... .40
Ulna:
Olecranon to distal end..... .635
Hind Limb:
Head of femur to D.IV, ph. 4.....2.23
Femur:
Head to endocondyle..... .950
Tibia:
Proximal to distal end..... .61
Fibula:
Proximal to distal end..... .63
Pelvic Girdle:
Prepubis, total length of..... .64
Prepubis, spread across right to left prepubes.....1.34
Postpubis, free portion of..... .36
Prepubis plus postpubis..... .86
Ischium.....1.05

AXIAL SKELETON

Length from rostrum to tip of caudals following curve.....7.08
Entire vertebral column following curves.....5.96

SKULL

Occipital condyle to rostrum.....1.12
Frill, top of, to base of manus.....2.30
Total length of, frill to rostrum.....1.95
Front of orbit to rostrum..... .855
Front of orbit to back of frill.....1.15
Frill, total width of.....1.25
Jaw:
Articular to predentaries..... .995
Horns:
Supra-orbital length, orbit to tip..... .83
Supranasal, height of..... .135
Width, supra-orbitals across tips..... .73

SPECIFIC REFERENCE.—The specific reference of the skull is to *Triceratops elatus* Marsh, by Dr. Richard S. Lull, the leading American authority on the Ceratopsia. He writes (letter, June 21, 1924): "I consider that the skull should be referred to *T. elatus* from the following characters: (a) the elevated parietal crest without marginal epoccipitals, which, however, may have been lost during fossilization, (b) the reduced nasal horns, (c) the forwardly directed supraorbital horns. *T. calicornis* Marsh is closely related to *T. elatus* if not conspecific. The mounted skull (Amer. Mus. 5116) is somewhat similar to that mounted in the National Museum; neither gives me the impression of the type of *Triceratops prorsus* in the New Haven Museum. As compared with *T.*

elatus, *T. prorsus* is distinguished by the following characters: (a) The nasal horn of *T. prorsus* is larger, (b) the rostrum does not extend so far in front of the nasal horn, (c) the parietal crest of *T. prorsus* is quite different, being deeply impressed with blood vessels which extend inwards on the inferior aspect for a distance of several inches from the periphery, (d) the epoccipitals are also present."

Pose of Mounted Skeleton

Pose of the Head.—The pose represents *Triceratops* charging with the head down and turned a little to the left as the animal drives forward. The head is slightly tipped to one side with the straight horns in a nearly horizontal position; this transmits the impact of the horns directly to the occipital condyles and the neck. This set of the skull, with the horns pointing directly forward at the object of attack, is obviously required by the mechanics of the action. The skull has a wide range of adjustment, pivoting on the joint of the condyles as a center, the whole skull forming a combination of pike and buckler in the occipital crest, very quickly adjusted to the needs of attack or of defense.

Pose of the Fore Limb.—The pose of the fore limb, set out widely apart from the body, is also designed to withstand attack, like the widely spreading feet of the pugilist or wrestler. With the humerus horizontal, the left foot reaches forward while the right foot is propelling the body just before it leaves the ground for the next step. The hind limb is totally unlike the fore limb in pose, the femur being subvertical as compared with the horizontal humerus, and the knee being only slightly everted. The hind and fore limbs are in alternating phases of the stride; the right hind limb reaches forward immediately behind the left fore limb, while the left hind limb reaches backward propelling the body strongly forward.

The widely spreading pose of the fore limb is the final result of a long series of experimental poses and of studies of numerous photographs not only of mammalian quadrupeds (for the action of the hind limb), but of iguanas, monitors, and other lizards, crocodiles and giant tortoises (for the action of the fore limb). After repeated attempts to pose the fore limb, with the humerus subvertical and the elbow more or less pointed backward (as in mammalian quadrupeds), it appeared, as observed by Dr. W. D. Matthew, "that neither of these poses could be worked out without disjointing the articulations in a quite impossible manner. Nothing short of a horizontal humerus and completely everted elbow would permit of proper articulation of the facets and place the

chief muscle processes and attachments in proper and mechanically possible relations. The fore limbs cannot be posed at all like those of a rhinoceros, nor apparently could the animal adopt the relatively straight position taken by a crocodile in running. The large lizards afford nearer parallel in the pose of the limb, while the tortoises appear to be the best guide for the feet. The tortoise has the humerus horizontal but reaching forward and outward from the shoulder-joint, while in *Triceratops*, the humerus reaches backward and outward but never forward at any phase of the stride.

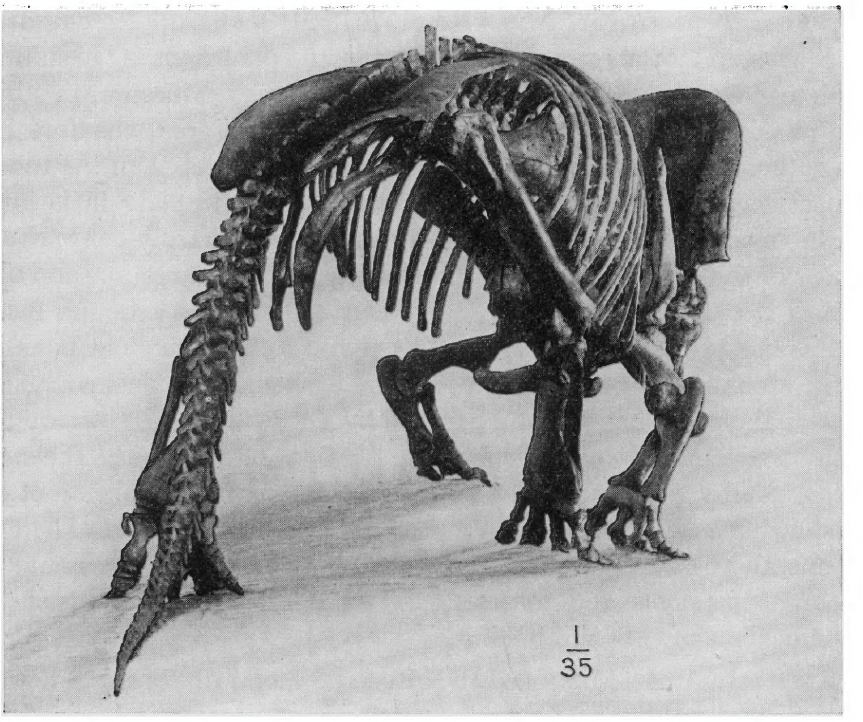

Fig. 3. *Triceratops elatus*, American Museum composite skeleton. Oblique rear view. One-thirty-fifth natural size.

"A large part of the forward and backward movement of the manus is accomplished through rotation of the humerus upon its axis. The remainder is a cumulation of the forward and backward movement of the humerus from the shoulder-joint, the forward and backward movement of the ulna and radius on the elbow-joint, and the movement of the metapodials on the wrist and of the phalanges on the finger-joints. A certain amount of twisting in the backbone and shoulder-girdle also adds to the

length of stride, which in spite of its apparent cramping by the limitations upon the movement of the humerus, is as long as that of the free-swinging hind limb. The heavy strain of supporting the great body on these widely-spread fore limbs is very apparent but there seems to be no other way to pose the skeleton. A compromise pose, such as that of the National Museum mounted skeleton (or of Marsh's restorations so far as they can be interpreted) serves to reduce, not to banish the anatomically impossible disjointing."

POSE OF THE FEET.—In the restoration of the fore limbs, the plaster reconstruction of the scapula, fore limb, and the foot, is chiefly based upon *Triceratops* (Amer. Mus. Nos. 970 and 973), supplemented by Amer. Mus. 971; the exact arrangement of the phalanges is based upon complete skeletons of *Monoclonius* in the American Museum, in which these phalanges are preserved in place. Thus restored, the fore feet have rather the short, flat character of the tortoise feet than the round, compact, cylindrical form of the mammalian quadruped; it is quite impossible to throw the metapodials into any such sharply convex form as those of the elephant, nor would the distal ends of the radius and ulna admit of it. There is, however, some convexity of the articular facets and this has been expressed by the facets and form of the foot bones.

SHOULDER GIRDLE.—The muscular relations of scapulae, coracoids, and sternal plates were carefully studied by Dr. William K. Gregory and rest upon several lines of evidence; the relations as seen in the skeletons of *Monoclonius* and others found in articulation; the contouring of the ribs, showing as generally among vertebrates a certain amount of hollowing beneath the swell of the subscapular muscle; the requirements for the throat passages and muscles, and especially the relations of the muscular attachments throughout.

RIBS.—In Amer. Mus. 5033 the fifteen presacral ribs of one side were preserved and not badly crushed, so that the restoration of the thorax in a natural curve is probably nearly correct. Agreeing with previous authors, Hatcher, Lull, and Gilmore, the vertebral column is arbitrarily divided into:

8 cervicals, the three anterior consolidated.
14 thoracics, with rib-bearing free centra.
10 sacrals, centra more or less consolidated.

The arrangement of the ribs on these thirty-two cervico-dorso-sacrals is as follows:

Atlas consolidated with cervicals 2–3. No rib known.
Axis consolidated, pleurapophysis, spine. First rib.

Cervical 3, bicipital rib and spine.

Cervicals 4–8 with bicipital ribs increasing rapidly in length.

Thoracics (=dorsals) 1–14 with bicipital ribs increasing in length to the 8th dorsal, diminishing in length to the 14th thoracic; 14th thoracic bicipital rib uniting superiorly with anterior border of ilium; 13th connected in its midsection with anterior border of prepubis. First sacral with vestigial rib beneath ilium.

Thus on these eight cervicals, fourteen thoracics and first sacral, we find all together remnants of *twenty-two* more or less complete ribs extending from the second cervical to the first sacral inclusive.

The thirteenth thoracic rib is especially important, since it forms a ligamentary connection near the middle of its length with the anterior end of the prepubis, the thickness of the bone for this articulation and the surface being very clearly marked. In previous mounts the prepubis has been placed inside the posterior rib.

THORAX.—The width of the thorax and position of the ribs are largely determined by the articulations of the head and tubercle; the final position given is as near as practicable to the sharp backward pitch of the ribs in most reptiles, differing considerably from the direct outward extension of the ribs in most herbivorous mammals. Thus the thorax of *Triceratops* retains the trihedral form characteristic of reptiles, with broad flat under surface extending backward from the flat coracoid-sternal portion of the shoulder girdle; and with sloping sides less strongly convex than in mammals. The narrow sternal region of most quadrupedal mammals is in contrast with these proportions.

PELVIS.—The sacrum and ilia are consolidated along with the adjacent dorso-sacral, the primary sacrals, and first caudo-sacral vertebrae (ten in all). The backward pitch of the ilium is conditioned by its articulation with the dorsal vertebrae and the natural curve of the presacral series, together with the relative height of the girdles as determined by the articulated fore and hind limb. It is more steeply pitched than in Marsh's restoration, somewhat more than in the National Museum mount, but it could not be articulated differently save through maladjustment of the vertebral facets, changes in the pose of the limbs or in the position of the scapula. The steep pitch of the ilia conforms well to the short and reduced caudal series. The ischia are not so much recurved distally as in the National Museum mount; the position of the pubes has already been noted.

HIND LIMB.—In contrast to the fore limb the hind limb bones are articulated with a subvertical femur, and the knee only a little everted. This corresponds to the mammalian pose and contrasts with the pose of

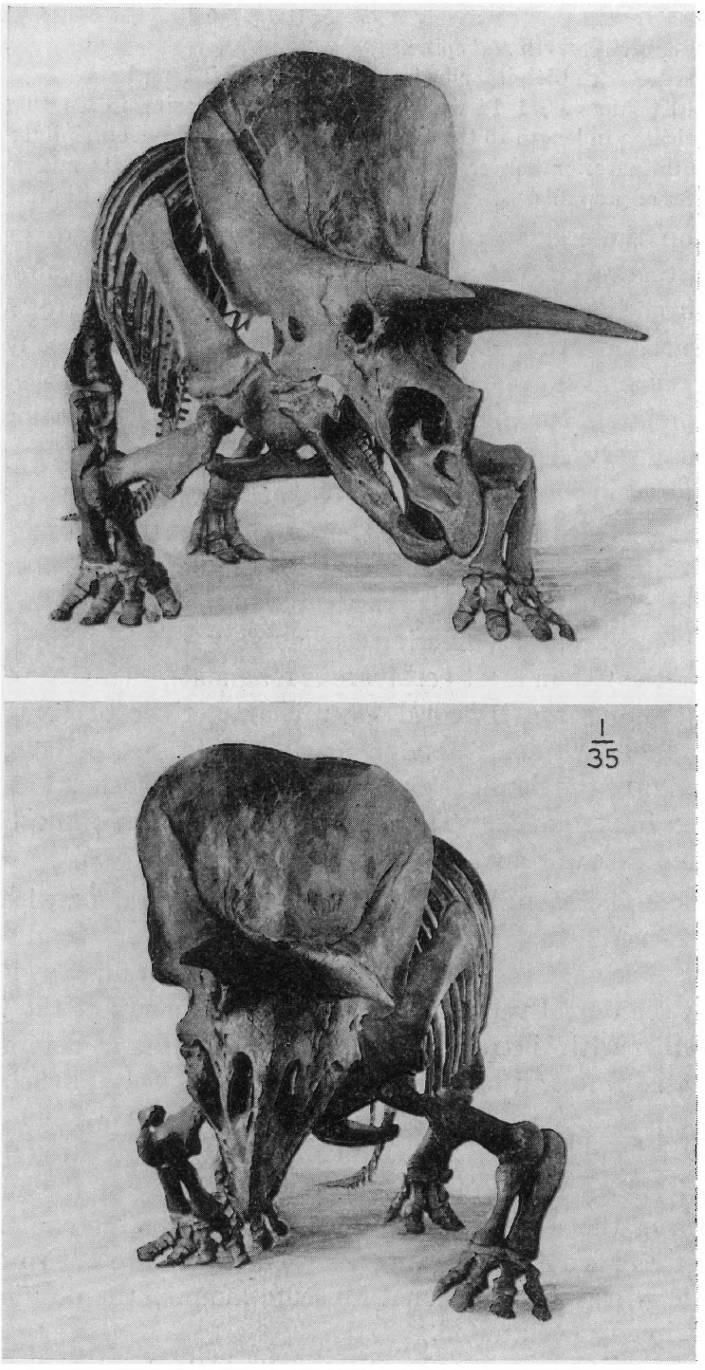

Fig. 4. *Triceratops elatus*, American Museum composite skeleton. Two anterior views. One-thirty-fifth natural size.

Fig. 5. Three views of *Triceratops elatus* model, made by Charles J. Lang.

lizards. The evidence is primarily the relations of the femoral joints and the position of the processes and attachments for the principal leg muscles. The head of the femur projects internally somewhat as in mammals, rather than proximad as in *Varanus* or *Iguana*, while the distal facets face chiefly distad instead of being limited to the posterior face of the bone as in these genera. A certain amount of eversion of the knee appears to be necessary to clear the swell of the posterior portion of the thorax, but the free fore-and-aft swing of the nearly straight hind limb is in marked contrast to the movements of the fore limb. The feet, however, seem to have been comparatively broad, short and spreading as in tortoises, not compactly rounded as in proboscideans. The pes is tetradactyl as in *Monoclonius* with the first four digits bearing hoofs; digit I with two phalanges, digit II with three phalanges, digit III with four phalanges, digit IV with five phalanges, and digit V represented by the reduced metatarsal.

Curvature of Backbone.—There is a double curve, as in mammals, unlike the straight run of the vertebrae in *Sphenodon*, lizards or crocodiles; but it is much less than in any of the restorations hitherto made. This alteration is based upon the actual fit of the centra; they are articulated with facets parallel and zygapophyses in place. This is regarded as the best evidence of the normal articular relations of the vertebrae. The curve adopted by Marsh in his restoration and in the mounted National Museum skeleton was presumably based upon the curvature of a series of vertebrae, *T. brevicornus* type (Yale Univ. Mus. 1834), as actually preserved in the rock (see Ceratopsia Monograph, 1907, Pl. XL). This curvature, however, must be regarded as probably corresponding to that usually seen in the various articulated dinosaur skeletons discovered in Montana and Alberta in recent years. As observed by Matthew and Brown (Amer. Mus. Novitates No. 89), these skeletons ordinarily have the backbone bent and the neck recurved dorsad, to the extreme limit of flexure. Although this is the usual position in the fossil skeleton, it is obviously not a normal position during life and should not be taken as a guide to the reconstructed skeleton.

Observation by Gregory and Matthew

The above notes on the special features of the pose in our mounted skeleton were largely supplied by Dr. W. D. Matthew. The following comments are added by Dr. William K. Gregory (letter June 24, 1924): "1. All the apparent anomalies in the fore and hind limbs of *Triceratops* (elbows widely everted, knees turned forward, mixture of lizard-like

and proboscidean suggestions) are entirely explicable by Dollo's theory that the Ceratopsia are secondarily quadrupedal, the gigantic descendants of small upright, running dinosaurs. The skeletal characters of *Protoceratops* are almost exactly intermediate between the two stages and furnish the keystone of palaeontological evidence in the cumulative morphological argument. 2. I do not find any mention of the new alignment of the bones surrounding the acetabulum, by means of which the acetabulum becomes a functionally effectve structure for articulation with the head of the femur. This new adjustment is also correlated with the new position of the prepubic process, which in our mount diverges sharply forward so as to encompass the abdominal cavity instead of sticking into the middle of it as in earlier restorations. Anteriorly the prepubic processes articulate with one of the presacral ribs, which have a peculiar sigmoidal flexure and a roughened surface apparently for contact with this process. One of our *Monoclonius* skeletons has the prepubic process actually in contact with this sigmoid rib. 3. The comparison of *Triceratops* with the quadruped rhinoceroses and proboscideans relates only to very superficial characters dependent upon vegetarian habits and huge bulk. All the nearest morphological resemblances in the pelvis and hind limbs are with birds, not with ungulates. 4. The *Triceratops* skeleton affords the most striking example of the concepts of habitus and heritage. The habitus characters, like later writings on a palimpsest, overlie and obscure the older characters or heritage. The habitus is the sum of all those characters which adapt the animal to its final peculiar mode of life; in this case, that of a gigantic herbivorous quadruped. The heritage is the sum of all those characters which it has received from an earlier mode of life; in this case, that of a small upright, running, *Psittacosaurus*-like, herbivorous ancestor of the Ceratopsia."

The time actually consumed in mounting this *Triceratops* skeleton is as follows:

Mr. Charles Lang	161½ days
Mr. Paul Bultman	102
Total number of days	263½ days

This includes restoring and mounting, but not the time spent in freeing the specimen from the matrix.

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